

# Biological control of locusts and grasshoppers: A review

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Academic editor: Ludivina Barrientos-Lozano | Received 20 October 2023 | Accepted 22 January 2024 | Published 5 November 2024

<https://zoobank.org/0ED8C5D6-0A15-4CA2-A2A1-D944851D372F>

Citation: Yasin M, Khan A, Qayyum MA, Yousuf HMB, Mehfooz A, Hunter D (2024) Biological control of locusts and grasshoppers: A review. Journal of Orthoptera Research 33(2): 289–304. <https://doi.org/10.3897/jor.33.114472>

## Abstract

Locusts and grasshoppers (Orthoptera: Acrididae) are pests of agricultural importance, devastating crops and pastures. This group includes hundreds of pest species and affects the livelihoods of one in every ten people worldwide. Their outbreaks can be chronic or episodic, with alternating periods of invasion and recession. Here, we review the natural enemies of locusts and grasshoppers in both their native and invaded ranges across the globe to assess the need for their conservation and maintenance as part of the natural suppression of outbreaks and to augment outbreak suppression as potential biological control agents. More than 70 natural enemies have been reported to attack locusts and grasshoppers, including entomopathogenic fungi, bacteria, nematodes, predatory insects, birds, reptiles, and mammals. Particular attention is given to the well-studied species of locusts and grasshoppers for which more information is available and to natural enemies in the locust-affected countries as part of the recent trend of looking for indigenous natural enemies. Such organisms can play a vital role in integrated pest management strategies for locusts and grasshoppers, particularly entomopathogens that can be incorporated with chemical pesticides into the management system. Among the organisms considered, *Metarhizium acridum* is noteworthy for inclusion in integrated pest management programs.

## Keywords

Agricultural pests, entomopathogens, integrated pest management, invasion, natural enemies, recession

## Introduction

Locusts and grasshoppers (L&G) are among the voracious insect pests belonging to the family Acrididae and mostly live in dry grassland and desert areas. Their economic importance is well established (Lomer et al. 2001, Song et al. 2018, Zhang et al. 2019). The family comprises about 10,000 species in the suborder

Caelifera and includes many potential pests of field crops, gardens, pastures, and forests (Usmani and Usmani 2018). L&G are polyphagous and profoundly different from other pests because of their rapid population increase to catastrophic levels, and the nymphal stages of some species congregate to form dense bands that have the potential to cause substantial losses in a very short time (Peng et al. 2020, Qayyum et al. 2024). The winged adults transform into swarms that can migrate over long distances of as much as hundreds of kilometers in a single day, invading previously uninfested regions and rapidly destroying vegetation and crops, resulting in major socio-economic losses on an international scale (Zhang et al. 2019). L&G outbreaks destroy the food sources of humans, animals, and wildlife, thus affecting food security and biodiversity. Losses due to these pests are not limited to damage to green vegetation; the resulting loss of vegetation cover results in increased runoff and soil erosion (Latchininsky 2008). From 2018 to 2020, Africa, the Middle East, and Southeast Asia experienced one of the most severe outbreaks of the desert locust, *Schistocerca gregaria* (Forskål, 1775 (Orthoptera: Acrididae)). In 2018, an outbreak began in the Arabian Peninsula with the first swarms seen in early 2019 and subsequently increasing and spreading by the end of the year to cover an area from the Horn of Africa to India/Pakistan, including Eritrea, Ethiopia, Kenya, Somalia, Saudi Arabia, Egypt, Yemen, Oman, Iran, Pakistan, and India (FAO 2020, World Bank 2020).

Most L&G control programs still revolve around treatments based on conventional chemical pesticides, including malathion, lambda-cyhalothrin, fipronil, etc. Injudicious use of these chemical pesticides has elicited many serious concerns related to the impact on human health, aquatic and terrestrial life, biodiversity loss, and hazards to environmentally sensitive areas such as waterways, national parks, inhabited areas, and so on (Henschel 2015). The harmful effects of chemical pesticides have led researchers toward



eco-friendly management tactics, including biological control as an important component of integrated pest management with a range of other management actions (Hunter 2004, Magor et al. 2008, Shi et al. 2019, Dakhel et al. 2020). The entomopathogens, together with predators, parasites, and parasitoids of locusts and grasshoppers, play a key role in regulating locust populations at low densities with minimum loss to biodiversity and fewer negative effects on human and animal health. Microbial control offers a reliable pest control method using entomopathogenic microorganisms, including fungi, bacteria, viruses, protozoa, nematodes, and microsporidia, which are derived from the natural environment and usually exhibit a significant degree of host specificity (Halouane et al. 2013). Globally, entomopathogens are used against a variety of insect pests with great advantage and success (St-Leger et al. 2009). Nowadays, fungal-based biopesticides are receiving substantial recognition in the control of L&G worldwide (Mullié and Guèye 2009, Sharma and Sharma 2021, Owuor and McRae 2022). They are considered very selective and have no negative impact on non-target species. Birds, amphibians, and reptiles do not leave sprayed areas, nor do they become intoxicated by the effects of the fungal-based biopesticides, and their populations often temporarily increase (Mullié 2007). This could be attributed to the fact that fungal-infected insects become sluggish and easy prey for birds. Thus, *Metarhizium acridum* (Hypocreales: Clavicipitaceae) enhances the impact of birds, and entomopathogens give evidence of synergetic effects in the case of birds (Mullié et al. 2021). Additionally, their integration with other control methods can be helpful in prolonging the effectiveness of control, as some entomopathogens, such as *Paranosema locustae* (Microsporidia), can become established within the host population (Zhang et al. 1995, Lange et al. 2020).

On the other hand, L&G are also known to be important to the food web of various organisms, especially small mammals (e.g., ground squirrels, shrews, and mice) (Churchfield et al. 1991, Russell and Detling 2003), birds (e.g., seagulls), and other insects (Dysart 1996). Since small mammals reproduce quickly and require large quantities of prey to fuel a rapid metabolism, they can be an excellent resource for limiting L&G populations (Churchfield et al. 1991). Consequently, the population of L&G can be regulated by natural enemies, particularly microbes, birds, and insects, keeping populations at low densities as part of maintaining a balanced ecosystem. If a population of natural enemies is removed from a particular ecosystem by any means (e.g., by non-selective insecticides), the L&G population has an increased chance of outbreaks, and once the L&G population increases, natural enemies are less effective in limiting their population. Here, we summarize the biocontrol agents associated with L&G by considering their potential in the integrated management of developing biological control strategies. Many studies on this subject have been conducted because of the importance of L&G pests.

### Microbial control of locusts and grasshoppers

*Entomopathogenic fungi (EPF).*—A comprehensive list of entomopathogenic fungi (EPF) collected from L&G is given in Table 1. Some of these entomopathogenic fungi have proven to be the most common and effective means of biological control of L&G populations, either through augmentative control of outbreaks or by inducing epizootics in L&G populations. Their mode of action contributes to their success in that, unlike other microorganisms, EPF do not need to be ingested and usually infect their host by direct contact with the host cuticle and penetrating the haemocoel through hyphal body penetration (Butt and Goettel 2000). The host can be

infected in several ways, i.e., through direct contact during spray application, subsequent pick-up from treated vegetation, horizontal transmission (a disease caused by infected to healthy insects), and vertical transmission (disease transmission through parents to offspring via transovarial or transovum transmission) (Kreutz et al. 2004, Zimmerman 2007, Jay et al. 2019). In the case of acridids, horizontal transmission does not happen regularly because of the requirement for very high humidity around the fungus-killed cadaver for several days. External sporulation among acridids is rare given their typical environment or due to contact with enough conidia contaminating the soil or phylloplane habitat of the insect. EPF are safer than chemical pesticides because of several biological traits, including host specificity, high reproductive rate and long-term survival, multiple infection cycles, and short generation time. These characteristics provide EPF with good potential as biocontrol agents against L&G (Sharma and Sharma 2021). Importantly, EPF-infected insects show sublethal effects, such as feeding cessation (Tefera and Pringle 2003) and reduced reproduction and survival potential of progeny (Dembilio et al. 2010, Wakil et al. 2022).

Currently, *M. acridum* is well known as a microbial control agent for L&G (Prior and Greathead 1989, Milner 2000, Aw and Hue 2017). Fungi of the genus *Metarhizium* are often the first choice among microbial control agents for inundative control. Moreover, molecular and biochemical analyzes have shown its wide distribution patterns ranging from the Arctic to the tropics and that it can colonize an impressive array of environments, including forests, savannahs, swamps, coastal zones, and deserts (Bidochka and Small 2005, Abro et al. 2019). US Environmental Protection Agency standards indicate that *M. anisopliae* has no impact on humans or other mammals in the field (Siegel 1997, Ahirwar and Singh 2023). Australia and China are successfully using entomopathogens against locusts and grasshoppers. About 15% of all locust control by the Australian Plague Locust Commission is done using *M. acridum*. In China, over 100,000 ha are sprayed with *M. acridum* and *Paranosema locustae* (Microsporidia) every year (Zhang et al. 2019). *M. acridum* is also used regularly as a control agent against locusts in Mexico (Poot-Pech et al. 2018) and was used to treat large areas (>100,000 ha) infested with desert locusts in Eastern Africa from 2020 to 2021 (Owuor and McRae 2022).

*Microsporidia.*—A comprehensive list of microsporidia collected from locusts and grasshoppers is given in Table 1. One particular microsporidian, *P. locustae* (Microsporidia), was the first microbial control agent developed for L&G control; previously, it was known as *Nosema locustae* and *Antonospora locustae* (Johnson 1997, Slamovits et al. 2004). In the early 1980s, *P. locustae* was developed as a biological control agent for L&G (Zhang and Lecoq 2021). More than 120 grasshopper species are susceptible to this pathogen (Lange 2005, Murray 2016). *P. locustae*, as an obligate parasite, reproduces in host target cells. Its infection involves the polar tube of the spore injecting its plasma into the target cells, causing high mortality in L&G. The pathogen's main target organ is the host's adipose tissue (fat body). *P. locustae* penetrates into the fat bodies of cells and produces meronts, sporonts, sporoblasts, and spores (Canning 1962, Solter et al. 2012). The pathogens' high capacity to sporulate in infected hosts, vertical disease transmission, and wider host range within the orthopteran insect order make them potential microbial control agents for L&G control in deserts and grasslands (Shi et al. 2009, 2018, 2019). While it has a broad host spectrum in Orthoptera, *P. locustae* is safer for non-orthopterans, humans, animals, and other non-target organisms (Menapace et al. 1978, Yuan et al. 2020, Zhang and Lecoq 2021).



*Entomopathogenic viruses (EPVs).*—Entomopathogenic viruses (EPVs) have been isolated from more than 1,000 insect species belonging to 16 families and from at least 13 different insect orders (Raj et al. 2022). They offer several advantages over conventional chemical pesticides, such as safety to non-target organisms, as well as being precise and ecologically stable. A comprehensive list of EPVs collected from locusts and grasshoppers is given in Table 1. The pathogenic potential of viruses has long been recognized, but interest in using viruses in biological insect pest control programs has increased over the last 40 years (Dakhel et al. 2020, Xu et al. 2022). For example, *Entomopoxvirus B* can infect 15 species of locusts and grasshoppers. The EPV of the migratory grasshopper *Melanoplus sanguinipes* (Fabricius, 1798) (Orthoptera: Acrididae) has been extensively investigated, and it can infect two related species: *M. differentialis* and *M. packardii* (Streett and McGuire 1990, Dakhel et al. 2020).

*Entomopathogenic bacteria (EPB).*—Entomopathogenic bacteria (EPB) are widely used against a wide variety of insect pests, with more than 90 species derived from natural resources (Waterfield and Daborn 2002, Azizoglu et al. 2020, Ali et al. 2022). EPB from the families Enterobacteriaceae, Bacillaceae, Streptococcaceae, Micrococcaceae, and Bacillaceae are insect pathogens. A comprehensive list of EPB collected from locusts and grasshoppers is given in Table 1. *Serratia marcescens* is an obligatory gram-negative bacterium that was originally isolated from the desert locust in Kenya and has proven effective against L&G in laboratories (Tao et al. 2006). Among the available EPB species, *Bacillus thuringiensis* is

the most common and widely used against insect pests. This gram-positive bacterium is extracted from plants, soil, and the guts of lepidopterous and coleopterous insects (Schünemann et al. 2014, Kumar et al. 2021). *B. thuringiensis* expresses two main types of protein toxins: crystal (Cry) and cytoplasmic (Cyt) (Kumar et al. 2021). Currently, there are 75 known crystal toxin subtypes that are highly specific to their target insects (Crickmore et al. 2020), and the endotoxin Crystal 7A is lethal against acridids (Song et al. 2008, Wu et al. 2011).

*Entomopathogenic nematodes (EPNs).*—Entomopathogenic nematodes (EPNs) are internal parasites of L&G and complete their development inside their hosts by feeding on hemolymph and tissue. Their presence can reduce fecundity, sterilize females, and eventually result in host death (Cranshaw 2008, Shairra 2009, Ghimire 2021, Fathy and Abd El-Rahman 2023). EPNs are obligate parasites that kill their hosts with the aid of mutualistic bacteria present in their intestines. They enter the host body through natural openings and release bacteria in the host gut; the bacteria tolerate the insects' cellular and non-cellular activities and inhibit immune responses (Youssef 2008, Fathy et al. 2023). The bacteria then multiply in the haemocoel and cause fatal septicemia (Jung and Kim 2007, Sharma et al. 2019). EPNs complete 2–3 generations in the host body, and infective juveniles come out of the host body to infect new hosts (Park and Kim 2000, Fathy and Abd El-Rahman 2023). A comprehensive list of nematodes collected from L&G is given in Table 1.

**Table 1.** Literature reports of microbial natural enemies collected from locusts and grasshoppers.

| Natural Enemy | Pathogen Sp.               | Acridid species                                                                           | Attacked stage  | Location of record | References                        |
|---------------|----------------------------|-------------------------------------------------------------------------------------------|-----------------|--------------------|-----------------------------------|
| Fungi         | <i>Metarhizium acridum</i> | <i>Locusta migratoria</i>                                                                 | Nymph           | China              | Liu et al. 2019                   |
|               |                            | <i>Schistocerca gregaria</i>                                                              | Adults          | United Kingdom     | Bateman et al. 1996               |
|               |                            | <i>Hieroglyphus daganensis</i> , <i>Oedaleus senegalensis</i> , <i>Kraussella amabile</i> | Nymph and adult | Africa             | Lomer et al. 1997a                |
|               |                            | <i>Locustana pardalina</i>                                                                | Adults          | South Africa       | Arthurs and Thomas 2000           |
|               |                            | <i>S. gregaria</i>                                                                        | Adults          | United Kingdom     | Arthurs and Thomas 2001           |
|               |                            | <i>S. gregaria</i>                                                                        | Nymphs          | Africa             | Tounou et al. 2008                |
|               |                            | <i>S. gregaria</i>                                                                        | Nymphs          | Mauritanie         | Etheimine et al. 2013             |
|               |                            | <i>S. gregaria</i>                                                                        | Nymph and adult | Africa             | Kamga et al. 2022                 |
|               |                            | <i>Dociostaurus maroccanus</i>                                                            | Adults          | Spain              | Valverde-Garcia et al. 2018, 2019 |
|               |                            | <i>L. migratoria</i>                                                                      | Adults          | Canada             | Ouedraogo et al. 2003             |
|               |                            | <i>Tropidacris collaris</i> , <i>Cornops frenatum frenatum</i> , <i>Parascopas obesus</i> | Adults          | Brazil             | Schmidt et al. 2018               |
|               |                            | <i>Uvarovistia zebra</i>                                                                  | Adults          | Iran               | Mohammadbeigi and Port 2015       |
|               |                            | <i>S. gregaria</i>                                                                        | Nymph           | Sudan              | Atheimine et al. 2014             |
|               |                            | <i>S. gregaria</i>                                                                        | Adults          | United Kingdom     | Blanford and Thomas 2001          |
|               |                            | <i>S. gregaria</i>                                                                        | Adults          | Niger              | Mulli   et al. 2021               |
|               |                            | <i>S. gregaria</i>                                                                        | Nymph           | Algeria            | Milat-Bissaad et al. 2011         |
|               |                            | <i>S. gregaria</i>                                                                        | Nymph           | Egypt              | Abdelatef et al. 2009             |
|               |                            | <i>S. gregaria</i> , <i>Euprepocnemis plorans</i>                                         | Nymph           | Egypt              | El-Maghraby et al. 2009           |
|               |                            | <i>L. migratoria</i>                                                                      | Adult           | China              | Zhang and Hunter 2005             |
|               |                            | <i>L. migratoria</i>                                                                      | Adult           | China              | Jiang et al. 2020                 |
|               |                            | <i>Patanga succincta</i>                                                                  | Nymph and adult | Thailand           | Sam  i    kov   and Purrini 1986  |
|               |                            | <i>Zonocerus variegatus</i>                                                               | Nymph and adult | Africa             | Chapman and Page 1979             |
|               |                            | <i>S. gregaria</i>                                                                        | Nymph and adult | Sweden             | Gunnarsson 1988                   |
|               |                            | <i>Poecillocerus pictus</i>                                                               | Adult           | Bangalore          | Ramanujam et al. 2022             |
|               |                            | <i>Oedaleus senegalensis</i>                                                              | Nymph and adult | Niger              | Langewald et al. 1999             |
|               |                            | <i>L. migratoria</i>                                                                      | Nymphs          | Russia             | Tokarev et al. 2011               |
|               |                            | <i>O. senegalensis</i>                                                                    | Adult           | Niger              | Blanford et al. 1998              |
|               |                            | <i>L. migratoria</i>                                                                      | Nymph           | Madagascar         | Welling et al. 1994               |
|               |                            | <i>S. gregaria</i> , <i>Hieroglyphus daganensis</i>                                       | Nymph and adult | Mali               | Caudwell and Gatehouse 1996       |
|               |                            | <i>Z. variegatus</i>                                                                      | Adults          | United Kingdom     | Thomas and Jenkins 1997           |



| Natural Enemy | Pathogen Sp.                  | Acridid species                                                           | Attacked stage  | Location of record        | References                                   |
|---------------|-------------------------------|---------------------------------------------------------------------------|-----------------|---------------------------|----------------------------------------------|
| Fungi         | <i>Metarhizium acridum</i>    | <i>H. daganensis, O. senegalensis, Kraussella amabile</i>                 | Nymph and adult | Africa                    | Lomer et al. 1997a                           |
|               |                               | <i>Melanoplus sanguinipes</i>                                             | Nymphs          | Canada                    | Inglis et al. 1997b                          |
|               |                               | <i>S. gregaria</i>                                                        | Adults          | France and United Kingdom | Prior et al. 1995                            |
|               |                               | <i>M. sanguinipes, L. migratoria, S. gregaria</i>                         | Adults          | Madagascar                | Nowierski et al. 1996                        |
|               |                               | <i>S. gregaria, Ornithacris cavroisi</i>                                  | Adult           | Africa - Asia             | Abraham et al. 1991                          |
|               | <i>M. flavoviridae</i>        | <i>S. gregaria</i>                                                        | Nymphs          | Mauritania                | Kooyman and Godonou 1997                     |
|               |                               | <i>H. daganensis</i>                                                      | Nymph and adult | Benin                     | Lomer et al. 1997a                           |
|               |                               | <i>P. vittatum</i>                                                        | Nymph and adult | Australia                 | Milner et al. 1994                           |
|               |                               | L&G                                                                       | Adult           | United Kingdom            | Thomas et al. 1995                           |
|               |                               | <i>H. daganensis, O. senegalensis, K. amabile</i>                         | Nymphs          | Niger, Mali               | Lomer et al. 1997b                           |
|               |                               | <i>Z. variegatus</i>                                                      | Adult           | Benin                     | Lomer et al. 1993                            |
|               |                               | <i>Ch. terminifera, P. vittatum</i>                                       | Nymph           | Australia                 | Milner and Prior 1994                        |
|               |                               | <i>S. gregaria</i>                                                        | Nymphs          | Mauritania                | Langewald et al. 1997                        |
|               |                               | <i>S. gregaria</i>                                                        | Adults          | United Kingdom            | Seyoum et al. 1994                           |
|               |                               | <i>Z. variegatus</i>                                                      | Adults          | Benin                     | Thomas et al. 1997                           |
|               | <i>M. brunneum</i>            | <i>L. pardalina</i>                                                       | Nymphs          | South Africa              | Price et al. 1997                            |
|               |                               | <i>R. schistocercoides</i>                                                | Nymph           | Brazil                    | Vicentini and Magalhaes 1996                 |
|               |                               | <i>S. gregaria</i>                                                        | Adult           | United State of America   | Moore et al. 1992                            |
|               |                               | <i>P. vittatum</i>                                                        | Adults          | Australia                 | Baker et al. 1994                            |
|               |                               | <i>Z. variegatus</i>                                                      | Adults          | Benin                     | Douro-Kpindo et al. 1995                     |
|               |                               | <i>S. gregaria</i>                                                        | Adult           | United Kingdom            | Bateman et al. 1993                          |
|               |                               | <i>S. americana</i>                                                       | Adult           | Africa                    | Sieglaff et al. 1998                         |
|               |                               | <i>Anabrus simplex</i>                                                    | Nymph           | USA                       | Foster et al. 2011                           |
|               | <i>M. robertsii</i>           | <i>M. sanguinipes</i>                                                     | Adult           | USA                       | Zembrzusi 2023                               |
|               | <i>Beauveria bassiana</i>     | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Marcandier and Khachatourians 1987           |
|               |                               | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Bidochka 1989                                |
|               |                               | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Bidochka and Khachatourians 1990, 1991, 1992 |
|               |                               | Grasshoppers                                                              | Nymph and adult | Mali                      | Johnson et al. 1992                          |
|               |                               | <i>S. gregaria</i>                                                        | Adults          | United Kingdom            | Bateman et al. 1996                          |
|               |                               | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Inglis et al. 1997a                          |
|               |                               | <i>M. sanguinipes</i>                                                     | Nymphs          | Canada                    | Inglis et al. 1997b                          |
|               |                               | <i>S. cancellata</i>                                                      | Adults          | South America             | Pelizza et al. 2020                          |
|               |                               | <i>M. sanguinipes</i>                                                     | Adults          | England                   | Marcandier and Khachatourians 1987           |
|               |                               | <i>M. sanguinipes</i>                                                     | Nymph           | Canada and Africa         | Inglis et al. 1996                           |
|               |                               | <i>Dociostaurus maroccanus</i>                                            | Adults          | Spain                     | Valverde-Garcia et al. 2018                  |
|               |                               | <i>S. gregaria, A. simplex</i>                                            | Nymph and adult | Pakistan                  | Wakil et al. 2022                            |
|               |                               |                                                                           | Nymph           | USA                       | Foster et al. 2011                           |
|               |                               | <i>Dichroplus maculipennis, Ronderosia bergii</i>                         | Nymph           | Argentina                 | Pelizza et al. 2023                          |
|               |                               | <i>Poekilocerus pictus</i>                                                | Adult           | Bangalore                 | Ramanujam et al. 2022                        |
|               |                               | <i>S. gregaria</i>                                                        | Nymph           | Algeria                   | Milat-Bissaad et al. 2011                    |
|               |                               | <i>S. gregaria</i>                                                        | Nymph           | Egypt                     | Abdelatef et al. 2009                        |
|               |                               | <i>S. gregaria E. plorans</i>                                             | Nymph           | Egypt                     | El-Maghraby et al. 2009                      |
|               |                               | <i>Uvarovistia zebra</i>                                                  | Adults          | Iran                      | Mohammadbeigi and Port 2015                  |
|               |                               | <i>L. migratoria, S. gregaria</i>                                         | Nymph           | Russia                    | Levchenko et al. 2020                        |
|               |                               | <i>Crassula pellucida, Malanoplus sp.</i>                                 | Adult           | USA                       | MacLeod 1954                                 |
|               |                               | <i>M. sanguinipes</i>                                                     | Nymph and adult | USA                       | Marcandier and Khachatourians 1987           |
|               |                               | <i>Trimerotropis pallidipennis, Dorycera maculipennis</i>                 | Nymph           | Argentina                 | Pelizza et al. 2023                          |
|               |                               | <i>M. sanguinipes</i>                                                     | Nymph and adult | Canada                    | Johnson and Goettel 1993                     |
|               |                               | <i>Cryptocatantops haemorrhoidalis, Acrotylus blondeli, H. daganensis</i> | Nymph and adult | Mali                      | Delgado et al. 1999                          |
|               |                               | <i>S. gregaria</i>                                                        | Nymphs          | Benin                     | Nasseh et al. 1992                           |
|               |                               | <i>L. migratoria</i>                                                      | Adult and nymph | Canada                    | Wu and Rozlomiy 2021                         |
|               | <i>B. brongniartii</i>        | <i>L. migratoria, S. gregaria</i>                                         | Nymph           | Russia                    | Levchenko et al. 2020                        |
|               |                               | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Khachatourians 1992                          |
|               | <i>B. cylindrospora</i>       | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Khachatourians 1992                          |
|               | <i>B. densa</i>               | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Khachatourians 1992                          |
|               | <i>Paecilomyces farinosus</i> | <i>M. sanguinipes</i>                                                     | Adult           | Canada                    | Khachatourians 1992                          |



| Natural Enemy | Pathogen Sp.                   | Acridid species                                                                               | Attacked stage  | Location of record        | References                                       |
|---------------|--------------------------------|-----------------------------------------------------------------------------------------------|-----------------|---------------------------|--------------------------------------------------|
| Fungi         | <i>Entomophaga grylli</i>      | <i>M. sanguinipes</i> , <i>M. bivittatus</i>                                                  | Adults          | Argentina Alberta, Canada | Erlandson et al. 1988, 2001, Pelizza et al. 2020 |
|               |                                | <i>Camnula pellucida</i>                                                                      | Nymph and adult | USA                       | Carruthers et al. 1997                           |
|               |                                | <i>C. pellucida</i> , <i>Dissosteira carolina</i> , <i>L. migratoria</i>                      | Nymph and adult | USA                       | Soper et al. 1983, Ramoska et al. 1988           |
|               |                                | <i>M. differentialis</i> , <i>C. pellucida</i>                                                | Adult           | USA                       | Ramoska et al. 1988                              |
|               |                                | <i>Hesperotettix speciosus</i> , <i>H. viridis</i>                                            | Adult           | USA                       | McDaniel 1986                                    |
|               |                                | <i>Camnula pellucida</i>                                                                      | Adult           | USA                       | Sawyer et al. 1997                               |
|               | <i>Aspergillus parasiticus</i> | <i>M. sanguinipes</i>                                                                         | Adult           | USA                       | Moore and Erlandson 1988                         |
|               | <i>A. oryzae</i>               | <i>L. migratoria</i>                                                                          | Nymph           | China                     | Zhang et al. 2015, You et al. 2023               |
|               | <i>Verticillium lecanii</i>    | Grasshoppers                                                                                  | Nymph           | United Kingdom            | Shah and Pell 2003                               |
|               |                                | <i>M. sanguinipes</i> , <i>M. bivittatus</i> , <i>M. packardii</i>                            | Adult           | Canada                    | Johnson et al. 1988                              |
|               | <i>Verticillium</i> spp.       | L&G                                                                                           | Nymph           | United Kingdom            | Shah and Pell 2003                               |
|               | <i>Hirsutella</i> spp.         | L&G                                                                                           | Nymph           | United Kingdom            | Shah and Pell 2003                               |
|               | <i>Entomophthora</i> spp.      | <i>S. gregaria</i>                                                                            | Adult nymph     | Egypt                     | Youssef 2014                                     |
|               | <i>Sorospora</i> sp.           | <i>L. migratoria</i>                                                                          | Nymph           | Madagascar                | Welling and Zimmerman 1997                       |
|               | <i>Paecilomyces</i> spp.       | <i>L. migratoria</i> , <i>S. gregaria</i> , <i>M. sanguinipes</i>                             | Adult           | Madagascar                | Nowierski et al. 1996                            |
| Microsporidia | <i>Paranosema locustae</i>     | <i>S. gregaria</i> , <i>E. plorans</i>                                                        | Nymph           | Egypt                     | El-Maghraby et al. 2009                          |
|               |                                | Grasshoppers                                                                                  | Nymph and adult | Mongolia                  | Dong 1989                                        |
|               |                                | <i>M. bivittatus</i>                                                                          | Nymph and adult | USA                       | Henry and Omar 1974.                             |
|               |                                | <i>Ceracris kiangsu</i>                                                                       | Nymph and adult | China                     | Chen et al. 2002                                 |
|               |                                | <i>Chondracris rosea</i>                                                                      | Nymph and adult | China                     | Liu and Chen 1996                                |
|               |                                | Grasshoppers                                                                                  | Nymph and adult | China                     | Ma et al. 2005                                   |
|               |                                | Grasshoppers                                                                                  | Nymph and adult | China                     | Chen et al. 2007                                 |
|               |                                | <i>S. gregaria</i>                                                                            | Nymph           | Africa                    | Tounou et al. 2008                               |
|               |                                | <i>S. gregaria</i> , <i>Oedaleus senegalensis</i>                                             | Nymph           | Africa                    | Tounou et al. 2011                               |
|               |                                | <i>S. cancellata</i>                                                                          | Nymph and adult | USA                       | Lange et al. 2000                                |
|               |                                | <i>Agropyron spicatum</i> , <i>A. smithiia</i> , <i>Artemisia frigid</i>                      | Nymph           | USA                       | Henry et al. 1973                                |
|               |                                | <i>L. migratoria</i>                                                                          | Nymph and adult | West African              | Canning 1962                                     |
|               |                                | <i>M. sanguinipes</i> , <i>M. packardii</i> , <i>Camnula pellucida</i>                        | Nymph and adult | Canada                    | Ewen and Mukerji 1980                            |
|               |                                | <i>L. migraioria</i> , <i>M. sanguinipes</i>                                                  | Adult           | USA                       | Henry 1969                                       |
|               |                                | Grasshoppers                                                                                  | Nymph           | China                     | Peng et al. 2018                                 |
|               |                                | <i>L. migratoria</i>                                                                          | Nymph and adult | China                     | Li et al. 2020                                   |
|               |                                | <i>S. cancellata</i> , <i>Dichroplus schulzi</i> , <i>Ronderosia bergii</i>                   | Nymph           | Argentina                 | Pocco et al. 2020                                |
|               |                                | Grasshoppers                                                                                  | Adult           | West Africa               | Henry et al. 1985                                |
|               |                                | <i>L. migratoria</i>                                                                          | Adult           | China                     | Li et al. 2020                                   |
|               |                                | <i>L. migratoria</i> , <i>S. gregaria</i>                                                     | Adult           | Russia                    | Tokarev et al. 2022                              |
|               |                                | <i>L. migratoria</i>                                                                          | Nymph           | Russia                    | Tokarev et al. 2011                              |
|               | <i>Nosema acridophagus</i>     | Grasshoppers                                                                                  | Nymph and adult | USA                       | Lange et al. 2020                                |
|               |                                | <i>M. sanguinipes</i>                                                                         | Adult           | USA                       | Erlandson et al. 1985                            |
|               |                                | <i>M. bivittatus</i> , <i>M. differentialis</i> , <i>S. americana</i>                         | Adult           | USA                       | Henry 1969                                       |
|               | <i>N. Cuneatum</i>             | <i>M. sanguinipes</i>                                                                         | Adult           | USA                       | Erlandson et at. 1988                            |
|               |                                | <i>M. differentialis</i>                                                                      | Adult           | USA                       | Henry 1971                                       |
|               |                                | <i>M. femurrubrum</i> , <i>S. americana</i>                                                   | Adult           | USA                       | Henry 1969                                       |
|               | <i>N. acridophagus</i>         | <i>M. sanguinipes</i>                                                                         | Adult           | USA                       | Erlandson et al. 1988, Erlandson et al. 2001     |
|               |                                | <i>M. bivittatus</i> , <i>M. differentialis</i> , <i>S. americana</i>                         | Adult           | USA                       | Henry 1969                                       |
|               |                                |                                                                                               |                 |                           |                                                  |
|               | <i>Malameba locustae</i>       | <i>L. pardalina</i>                                                                           | Adult           | Africa and USA            | Prinsloo 1960, Henry 1968                        |
|               |                                | <i>M. sanguinipes</i>                                                                         | Adult           | Canada                    | Hinks and Ewen 1986                              |
|               | <i>N. acridophaga</i>          | <i>M. sanguinipes</i>                                                                         | Adults          | USA                       | Boorstein and Ewald 1987                         |
|               | <i>N. entomophaga</i> ,        | L&G                                                                                           | Nymph           | Argentina                 | Johnson 1997                                     |
|               | <i>Johenrea locustae</i>       | <i>L. migratoria</i>                                                                          | Nymph           | Madagascar                | Lange et al. 1996                                |
|               | <i>Perezia dichroplusa</i>     | <i>Dichroplus elongata</i>                                                                    | Adult           | South America             | Lange 1987                                       |
|               | <i>N. acridophagus</i>         | <i>M. bivittatus</i>                                                                          | Nymph and adult | USA                       | Henry and Omar 1974                              |
|               | <i>N. cureatum</i>             | <i>M. bivittatus</i>                                                                          | Nymph and adult | USA                       | Henry and Omar 1974                              |
| Virus         | Nuclear Polyhedrosis           | <i>S. americana</i>                                                                           | Adults          | Egypt                     | Mahmoud and Soliman 2015                         |
|               | Virus (NPV)                    | <i>M. sanguinipes</i> , <i>M. bivittatus</i> , <i>M. differentialis</i> , <i>S. americana</i> | Adult           | USA                       | Henry and Jutila 1966                            |



| Natural Enemy | Pathogen Sp.                                                          | Acridid species                                                                                                                                                                                                                                                             | Attacked stage  | Location of record | References                                  |
|---------------|-----------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------|--------------------|---------------------------------------------|
| Virus         | Nuclear Polyhedrosis Virus (NPV)                                      | <i>L. migratoria</i> , <i>S. gregaria</i>                                                                                                                                                                                                                                   | Nymph           | Israel             | Bensimon et al. 1987, Faktor and Raviv 1996 |
|               |                                                                       | <i>S. americana</i>                                                                                                                                                                                                                                                         | Adult           | Egypt              | Mahmoud and Soliman 2015                    |
|               |                                                                       | <i>M. sanguinipes</i> , <i>M. bivittatus</i> ,<br><i>M. differentialis</i> , <i>S. americana</i>                                                                                                                                                                            | Adult           | USA                | Henry and Jutila 1966                       |
|               | Entomopoxvirus                                                        | <i>L. migratoria</i> , <i>S. gregaria</i>                                                                                                                                                                                                                                   | Nymph           | Israel             | Bensimon et al. 1987, Faktor and Raviv 1996 |
|               |                                                                       | <i>M. sanguinipes</i> , <i>Phoetaliotes nebrascensis</i> , <i>Arphia conspersa</i>                                                                                                                                                                                          | Nymph           | USA                | Langridge et al. 1983                       |
|               |                                                                       | <i>Cataloipus fuscocoeruleipes</i>                                                                                                                                                                                                                                          | Nymph and Adult | Yemen              | Purrini 1989                                |
|               |                                                                       | <i>S. gregaria</i> , <i>Chortipes</i> sp.                                                                                                                                                                                                                                   | Nymph and Adult | Africa-Asia        | Purrini and Rohde 1988                      |
|               |                                                                       | <i>L. migratoria</i>                                                                                                                                                                                                                                                        | Nymph and Adult | Africa-Asia        | Purrini et al. 1988                         |
|               |                                                                       | <i>Oedaleus senegalensis</i> , <i>O. nigeriens</i> ,<br><i>Kraussaria angulifera</i> , <i>Heteracris annulosus</i> , <i>Spharagemon collare</i> ,<br><i>Xanthippus corallipes</i> , <i>Psoloessa delicatula</i> , <i>Encoptolophus sordidus</i> ,<br><i>P. nebrascensis</i> | Adult           | Senegal, USA       | Henry et al. 1985                           |
|               |                                                                       |                                                                                                                                                                                                                                                                             |                 |                    |                                             |
|               | Small RNA virus                                                       | <i>Melanoplus bivittatus</i>                                                                                                                                                                                                                                                | Nymph and adult | USA                | Jutila et al. 1970                          |
| Bacteria      | <i>Malpighamoeba locusta</i>                                          | <i>M. differentialis</i> , <i>M. mexicanus</i> ,<br><i>M. femurrubrum</i>                                                                                                                                                                                                   | Adult           | USA                | Taylor and King 1937                        |
|               | <i>Bacillus weihenstephanensis</i> ,<br><i>Pseudomonas aeruginosa</i> | <i>S. gregaria</i>                                                                                                                                                                                                                                                          | Nymph           | Egypt              | Mashtoly et al. 2019                        |
|               | <i>B. cereus</i>                                                      | <i>S. gregaria</i>                                                                                                                                                                                                                                                          | Nymph           | Egypt              | Reda et al. 2018                            |
|               | <i>Coccobacillus acridiorum</i>                                       | Grasshoppers                                                                                                                                                                                                                                                                | Nymph and adult | Mexico             | Lord 2005                                   |
|               | <i>Serratia marcescens</i>                                            | <i>S. gregaria</i>                                                                                                                                                                                                                                                          | Nymph and adult | UK                 | Bundey et al. 2003                          |
|               | <i>B. thuringiensis</i>                                               | L&G                                                                                                                                                                                                                                                                         | Nymph           | Germany            | Zelazny et al. 1997                         |
|               | <i>Rickettsiella grylli</i>                                           | <i>S. gregaria</i>                                                                                                                                                                                                                                                          | Adult           | Africa-Asia        | Vago and Martoja 1963                       |
|               |                                                                       | <i>L. migratoria</i>                                                                                                                                                                                                                                                        | Adult           | Africa-Asia        | Vago and Martoja 1963                       |
|               |                                                                       | <i>Zonocerus variegatus</i> ,<br><i>M. sanguinipes</i> , <i>M. differentialis</i>                                                                                                                                                                                           | Adult           | Senegal            | Henry et al. 1986                           |
|               | <i>R. schistocerc</i>                                                 | <i>S. gregaria</i> , <i>L. migratoria</i>                                                                                                                                                                                                                                   | Adult           | Africa-Asia        | Vago and Meynadier 1965                     |
| Nematodes     | <i>Hexameris</i> sp.                                                  | Grasshoppers                                                                                                                                                                                                                                                                | Nymph           | America            | Puttler and Thewke 1971                     |
|               | <i>Agameris ecaudate</i><br><i>Mermis subnigrescens</i>               | L&G                                                                                                                                                                                                                                                                         | Adult           | America            | Rees 1973                                   |
|               | <i>M. nigrescens</i> ,<br><i>Gordius robustus</i>                     | Grasshoppers                                                                                                                                                                                                                                                                | Adult           | USA                | Cranshaw 2008                               |
|               | <i>Steinernema carpocapsae</i>                                        | <i>S. gregaria</i>                                                                                                                                                                                                                                                          | Nymph and adult | Egypt              | Youssef 2014                                |
|               | <i>Henlea lefroyi</i>                                                 | Locusts                                                                                                                                                                                                                                                                     | Adult           | Thailand           | Usmani and Usmani 2018                      |
|               | <i>M. quirindiensis</i>                                               | <i>P. vittatum</i> , <i>Praxibulus</i> sp.,<br><i>Chortoicetes terminifera</i>                                                                                                                                                                                              | Nymph and adult | Australia          | Baker and Poinar Jr 1986                    |
|               |                                                                       |                                                                                                                                                                                                                                                                             |                 |                    |                                             |

Arthropods and vertebrates as natural enemies of locusts and grasshoppers

Consideration of the population dynamics of L&G leads to a focus on biological control options using non-microbial control agents, such as arthropods and vertebrates. Up to 70–80% of the first instar stage L&G can die due to inadequate water reserves, cannibalism, and predation by ants. Different ants, parasitic wasps, predatory beetles, reptiles, and birds feed on locust hoppers (Zhang and Hunter 2017, Zhang et al. 2019).

*Insects*.—Parker and Wakeland (1957) estimated that an average of 19% of L&G egg pods are destroyed by predators and that, at the local level, mortality may be as high as 100%. Acridid egg pods can also be destroyed by the larvae of bee flies, blister beetles, and ground beetles (Parker and Wakeland 1957, Ghoneim 2013). The insects that feed on grasshopper eggs can be divided into two groups—predators and parasitoids—based on the insects’ feeding method. Egg predators attack the eggpod as a whole, feeding externally on the grasshopper eggs.

Predators are capable of moving from one egg or eggpod to another as they complete their development. *Anastoechus angustifrons* Paramonov, 1930 (Diptera: Bombyliidae) are predators of grasshopper eggs. The larvae of blister beetles (meloids) are an important group of predators of grasshopper eggs, and while the larvae are predaceous, the adults feed exclusively on vegetation (Ghahari et al. 2009, Shanklin et al. 2010, Ghoneim 2013). Parasitoids feed internally and complete their development within a single egg. In general, parasitoids of the eggs of insects are usually tiny hymenopterous wasps of the family Scelionidae (Baker et al. 1996). The most important genus is *Scelio* (Latreille, 1805) the hymenopterous egg parasitoid with the greatest potential for use as a successful biological control agent (Greathead 1992). Khajehzadeh and Ghazavi (2000) reported that the parasitoid *Scelio flavibarbis* (Marshall, 1874) infests 27% of egg capsules, destroying some 4–16% of the eggs of the migratory locust, while Hunter et al. (1998) reported parasitism rates of as much as 50% of the eggs of the Australian plague locust.

*Mites*.—One of the important biological checks on grasshopper numbers is the grasshopper mite, *Eutrombidium trigonum*



Table 2. Literature reports of arthropod and vertebrate that are natural enemies of locusts and grasshoppers.

| Natural Enemy | Predator species                                                                               | Acridid species | Attacked stage         | Location of record      | References                             |
|---------------|------------------------------------------------------------------------------------------------|-----------------|------------------------|-------------------------|----------------------------------------|
| Insects       | Meloid beetles, Bombylid flies, <i>Scelio pambertoni</i> , <i>S. parvicornis</i>               | Grasshoppers    | Eggs                   | Africa                  | Greathead 1992, Dysart 1996            |
|               | <i>S. flavibarbis</i>                                                                          | L&G             | Eggs                   | North America           | Ghahari et al. 2009                    |
|               | <i>Hylemya cilirura</i>                                                                        | Locusts         | Nymph                  | Pakistan                | Usmani and Usmani 2018                 |
|               | <i>Acridomyia canadensis</i>                                                                   | Grasshoppers    | Adult                  | Canada                  | Rees 1973                              |
|               | <i>Hylemya angustifrons</i>                                                                    | Grasshoppers    | Eggs                   | Canada                  | Hostetter 1994                         |
|               | <i>Neorhynchocephalus sackenii</i>                                                             | Grasshoppers    | Nymph and adult        | North American          | Prescott 1960, Smith 1958              |
|               | <i>Mantis religiosa</i>                                                                        | Grasshoppers    | Nymph                  | British Columbia        | Cannings 2007                          |
|               | <i>Pterostichus gebleri</i>                                                                    | Grasshoppers    | Nymph and adult        | China                   | Shi et al. 2018                        |
|               | <i>Telenomus</i> sp.                                                                           | L&G             | Eggs                   | China                   | Ji et al. 2008                         |
|               | <i>Blaesoxipha pachytyli</i> ,<br><i>Trichopsidea ostracea</i>                                 | Locusts         | Eggs and nymph         | Australia               | Baker 1995                             |
|               | <i>Scelio</i> spp.                                                                             | L&G             | Egg                    | Australia               | Baker et al. 1996                      |
|               | <i>Phiddipus audax</i>                                                                         | Grasshoppers    | Nymph and adult        | USA                     | Maloney et al. 2003                    |
|               | <i>Pardosa monticola</i>                                                                       | Grasshoppers    | Nymph                  | UK                      | Cherrill and Begon 1989                |
| Spiders       | <i>Xysticus cristatus</i>                                                                      | Grasshoppers    | Nymph                  | British                 | Richards and Waloff 1954               |
|               | Lycosidae spiders                                                                              | Grasshoppers    | Adult                  |                         | Oedekoven and Joern 2000               |
|               | <i>Rabidosa rabida</i>                                                                         | Grasshoppers    | Nymph and adult        | USA                     | Maloney et al. 2003                    |
|               | <i>Agelena labyrinthica</i>                                                                    | Grasshoppers    | Adult                  | USA                     | Young and Edwards 1990                 |
|               | <i>Trochosa parthenus</i>                                                                      | Grasshoppers    | Adult                  | USA                     | Punzo and Kukoyi 1997                  |
|               | <i>Eutrombidium locustarum</i>                                                                 | Grasshoppers    | Eggs                   | North America           | Husband and Wohltmann 2011             |
|               | <i>Podapolipus</i> sp.                                                                         | Locusts         | Adult                  | Thailand                | Usmani and Usmani 2018                 |
| Mites         | <i>Astoma locustarum</i>                                                                       | Grasshoppers    | Eggs and adult         | North America           | Walsh 1860                             |
|               | <i>Eutrombidium trigonum</i>                                                                   | Grasshoppers    | Eggs, nymph, and adult | USA                     | Severin 1944                           |
|               | <i>Uromastix hardwickii</i>                                                                    | Locusts         | Nymph                  | Rajasthan               | Usmani and Usmani 2018                 |
|               | <i>Acanthodactylus cantoris</i>                                                                | Locusts         | Nymph                  | Rajasthan               | Usmani and Usmani 2018                 |
| Reptiles      | <i>Eremias argus</i>                                                                           | Grasshoppers    | Nymph                  | China                   | Xunbing et al. 2016                    |
|               | <i>E. argus</i>                                                                                | Grasshoppers    | Nymph                  | Mongolia                | Huang et al. 2016                      |
|               | <i>Bufo bufo</i>                                                                               | Grasshoppers    | Adult and nymph        | United State of America | Dellonger and Day 2021                 |
|               | <i>Acridotheres tristis</i>                                                                    | Locusts         | Adult                  | India                   | Long 1981                              |
|               | <i>Pastor roseus</i>                                                                           | L&G             | Nymph and adult        | Russia                  | Belik and Mihalevich 1994              |
| Birds         | <i>Ciconia ciconia</i> , <i>Glareola nordmanni</i>                                             | Locusts         | Adult                  | Africa                  | Lounsbury 1909                         |
|               | <i>Milvus migrans</i> , <i>Corvus alba</i> ,<br><i>Falco naumanni</i> , <i>Circus pygargus</i> | L&G             | Nymph and adult        | Niger                   | Falk et al. 2006, Petersen et al. 2008 |
|               | <i>Chelictinia riocourii</i>                                                                   | Locusts         | Nymph and adult        | Africa                  | Pilard 2007, Mullié 2009               |
|               | <i>Sturnus roseus</i>                                                                          | Grasshoppers    | Nymph and adult        | China                   | Ji et al. 2008                         |
|               | <i>Passer luteus</i>                                                                           | Locusts         | Nymph                  | Mauritania              | Kooyman et al. 2008                    |
|               | <i>Corvus splendens</i>                                                                        | Locusts         | Adult                  | India                   | Usmani and Usmani 2018                 |
|               | <i>Egertta alba</i>                                                                            | Locusts         | Adult                  | Africa                  | Sanyang 2001                           |
|               | <i>Onychomys leucogaster</i> ,<br><i>Spermophilus tridecemlineatus</i>                         | Grasshoppers    | Adult                  | United State of America | Stevens 1989                           |
|               | <i>Procyon lotor</i>                                                                           | Grasshoppers    | Nymph and adult        | United State of America | Dellonger and Day 2021                 |
|               | <i>Vulpes velox</i>                                                                            | Grasshoppers    | Nymph and adult        | United State of America | Nevison and Day 2018                   |
| Mammals       | <i>Cynomys ludovicianus</i>                                                                    | Grasshoppers    | Nymph and adult        | United State of America | Russell and Detling 2003               |
|               | <i>Homo sapiens</i>                                                                            | Locusts         | Nymph and adult        | Pakistan, Mexico, India | Samejo et al. 2021                     |

(Hermann, 1804) (Acari: Microtrombidiidae). In its larval stage, it is parasitic on grasshoppers, and in its nymphal and adult stages, it is predaceous on the eggs of grasshoppers (Severin 1944, Sevsay and Karakurt 2013, Gupta and Kumar 2018). Previous studies suggest that mite larvae reduce grasshopper fecundity and mobility, making them useful for the integrated pest management of grasshopper populations (Anderson 2019).

*Spiders.*—Although the spiders (Araneae) are a diverse arachnid order consisting of more than 3,500 species in North America (Young and Edwards 1990, Duperre 2023), all are obligate predators, and many feed upon herbivorous pest insects (Dellonger and Day 2021). The orb-web weavers Araneidae and Tetragnathidae feed upon Homoptera, such as leafhoppers, Diptera, and Orthoptera, especially grasshoppers (Nyffeler et al. 1994, Moses et al. 2022). The spiders are probably the least studied of the L&G predators. Nine species of spiders have been reported as predators of grasshoppers, but the list is known to be incomplete and is undoubtedly much longer. The wolf spider, *Schizocosa minnesotensis* Gertsch, 1934), and a jumping spider, *Pellenes* sp., are two species of non-web builders that are often quite abundant on rangelands and are reported as predatory on



various rangeland grasshopper species (Lavigne and Pfadt 1966, Mishra et al. 2021).

**Birds.**—Birds can reduce acridid densities by 30–50%. A survey of published accounts and other relevant sources conducted by Mullié (2009) revealed that at least 537 bird species from 61 families are currently known to prey on L&G in Africa. Several African bird families, such as Coraciidae and Laniidae, appear to be specialized acridivores (Yang and Gratton 2014, Kollross et al. 2023). A wide range of acridid species are recorded as food for Ciconiidae, Glareolidae, and Corvidae (Dellonger and Day 2021). Petersen et al. (2008) and Falk et al. (2006) found that the pre-migratory movements of Abdim's storks are in synchrony with the seasonal movements of Senegalese grasshoppers. Over 200 species of birds (e.g., grassland bird species) feed on grasshoppers (Wang et al. 1998, McEwen et al. 2000) and can aid in managing grasshopper populations. Sick and dying grasshoppers and locust hoppers, rendered sluggish by *Metarhizium*, have also been seen being taken by birds and frogs (Kooyman et al. 2003, Mullié 2021, Mullié et al. 2021). Many field experiments have shown that avian predation can substantially impact grasshopper populations (Branson 2005, Ji et al. 2008). In some areas of India and Pakistan, rose-colored starlings were claimed to have eliminated 50% or more of desert locust hopper bands. China is one of the few countries where bird predation, either natural or by herded ducks and chickens, is actively used as a very important contribution to biological locust control (Zhang and Hunter 2017, Shi et al. 2019).

**Amphibians, reptiles, and mammals.**—Locust remains found in droppings indicate that some mammals, such as foxes, skunks, opossums, raccoons, Japanese macaques, and geladas, also eat locusts (Price and Mitchell 2003, Kooyman et al. 2003). L&G are known for being important to the food web of various organisms, especially small mammals (e.g., ground squirrels, shrews, and mice) (Churchfield et al. 1991, Russell and Detling 2003, Dellonger and Day. 2021). Since small mammals reproduce quickly and require large quantities of prey to fuel a rapid metabolism, they can be an excellent resource for managing grasshopper and locust populations (Churchfield et al. 1991). Moreover, toads, frogs, lizards, and snakes also prey on L&G (Dellonger and Day. 2021).

## Conclusion

Many varieties of natural enemies of L&G exist in nature, which underscores the complexity of the ecological relationships within these ecosystems. L&G cause substantial agricultural losses and environmental damage. Intricate networks of pathogens, parasites, and predators keep their populations below a certain level. At present, there are commercial formulations of entomopathogenic fungi, i.e., *Metarhizium acridum*, Green Guard® (Australia), Green Muscle® (UK, Africa), Novacrid® (Africa) and Metacridium® (Mexico). *Paranosema locustae* is formulated and commercially available in China. In this review, we explored the natural enemies of L&G, each playing a unique role in regulating their populations. Natural enemies are not only promising biocontrol agents but also help maintain ecological balance. By preserving their natural habitats and providing favorable conditions, we can foster ecologically sound and environmentally friendly management of L&G. Moreover, integrating these natural enemies with other sustainable pest control practices can reduce reliance on chemical pesticides to safeguard agricultural productivity and promote healthier ecosystems.

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